On the ecological genetics of the clonal perennial Agrostis stolonifera

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SUMMARY

There have to date been few studies specifically addressed to the evolution of clonal organisms. The present study attempts to fill this gap and aims to analyse the distribution pattern of a clonal plant species, using the wide-spread grass *Agrostis stolonifera* L.(Creeping Bent) as a model species. A genecological approach was chosen because the question of what limits the distribution of a species is an ecological as well as an genetical one.

One of the marked characteristics of clonal plants, is the occasionally extensive clonal replication in populations causing them to exist of only one or two clones. Most of the studies did not take this important feature of clonal plant populations into account and made population analyses on the ramet (tiller) level. It is, however, of fundamental importance to know the genotypic composition of populations to consider evolutionary questions. In this study the genotypic composition of populations was established by means of protein electrophoresis.

Four ecologically largely contrasting population of *Agrostis stolonifera* were studied in detail, namely an inland meadow, a salt marsh, a polder and a sand dune population. The first two populations were considered non-colonizing. Both populations differed, however, in the factors determining population numbers. In the inland meadow population biotic factors (competition) primarily determine population numbers, whereas in the salt marsh population abiotic factors (salt, inundation) play a more important role. The polder and sand dune population were considered colonizing. The polder population, located on an embanked sandflat, is known not to have colonized the area before 1970. Selection pressures are moderate due to the continuing desalination process and intermediate levels of macro-nutrients and soil moisture. The sand dune population seems to be in a permanent stage of colonization, because the environment is mostly harsh due to extremely low levels of macro-nutrients, soil moisture and shifting sand.

The general approach analysing these populations was to make comparisons within and between populations in controlled environments (experimental garden and greenhouse) as well as in natural habitats. The use of the same genotypes in both experimental and natural environments provided the opportunity to test the hypotheses based on observations under controlled conditions, in natural habitats.

Large clonal population differentiation was observed among the four populations which were studied.

The first major contrast among populations was the extent to which they reproduced sexually. The inland meadow reproduced mainly asexually, whereas the polder and sand dune population also had a strong sexual component. The salt marsh population took an intermediate position. The differences are probably caused by differences in the cytotype composition of the

populations studied. It was known from other previously performed studies that *Agrostis stolonifera* is a polyploid complex with more sexually reproducing tetraploids and more asexually reproducing penta- and hexaploids. The inland meadow population proved to have predominantly cytotypes with chromosome complements higher than the tetraploid complement, the salt marsh and polder populations consisted mainly of the tetraploid cytotype, whereas the sand dune population only comprised the tetraploid cytotype. The observed somatic variation in number of chromosomes (aneusomaty), especially in the inland meadow population, was noteworthy. The differences in sexuality among the populations most likely reflect the response to the environments faced by each of the populations seperately. The inland meadow population faces more stable environmental conditions with high vegetation densities, resulting in an increase of the more competitive cytotypes, *i.e.* the non-tetraploids. The other populations were generally affected by more unpredictable environmental conditions which resulted in the increase of more sexually reproducing cytotypes, *i.e.* the tetraploids.

The second major contrast among populations was the difference in clonal architecture (*i.e.* the morphological design of a clone) and growth rate. The clones from the inland meadow population had a few, long and thick stolons, a high relative growth rate (RGR) under mineral-rich conditions and a high response to changes in mineral conditions. The salt marsh clones had numerous, short and thin stolons, while clones from the sand dune had a few, long and thin stolons, a high RGR under nutrient-limiting conditions and a low response to changes in mineral conditions. The polder population consisted of a mixture of architectural types, and had consequently an intermediate RGR and response. The aforementioned differences in clonal architecture and growth rate (both important elements of the growth strategy) might be a result of the response to the heterogeneity of the habitat. Relatively few good patches (*e.g.* light and nutrients) are available in the inland meadow and sand dune habitat. Selection, therefore, acts in favour of clones with an increased search capacity. In the salt marsh site most patches are equal due to the levelling influence of the sea. Persistence rather than search capacity is thought to be at a premium in this site.

The differences among populations in clonal structure (*i.e.* the spatial arrangement of clones in a population) as detected by means of protein electrophoresis corresponds well with the differences in sexuality and growth strategy observed among populations. In the inland meadow population only a few extremely replicated clones were found, whereas an increased number of generally small clones were found in the other populations.

Reciprocal transplant experiments of single tillers from populations into each others habitat showed that populations can not only survive and reproduce in their own native habitats, but also in alien ones. It is, therefore, argued that the evolutionary success of *Agrostis stolonifera* is not only due to genetic differentiation, but also to a considerable extent to phenotypic plasticity.